# The energy-signalling hub SnRK1 is important for sucrose-induced hypocotyl elongation

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**Running title:** Sucrose-induced hypocotyl elongation

**Abstract**

Emerging seedlings respond to environmental conditions such as light and temperature to optimize their establishment. Seedlings grow initially through elongation of the hypocotyl, which is regulated by signalling pathways that integrate environmental information to regulate seedling development. The hypocotyls of *Arabidopsis thaliana* also elongate in response to sucrose. Here, we investigated the role of cellular sugar-sensing mechanisms in the elongation of hypocotyls in response to sucrose. We focused upon the role of SnRK1, which is a sugar-signalling hub that regulates metabolism and transcription in response to cellular energy status. We also investigated the role of TPS1, which synthesizes the signalling sugar trehalose-6-phosphate (Tre6P) that is proposed to regulate SnRK1 activity. Under light/dark cycles, we found that sucrose-induced hypocotyl elongation did not occur in *tps1* mutants and overexpressors of KIN10 (AKIN10/SnRK1.1), a catalytic subunit of SnRK1. We demonstrate that the magnitude of sucrose-induced hypocotyl elongation depends on the day length and light intensity. We identified roles for auxin and gibberellin signalling in sucrose-induced hypocotyl elongation under short photoperiods. We found that sucrose-induced hypocotyl elongation under light/dark cycles does not involve another proposed sugar sensor, HEXOKINASE1, or the circadian oscillator. Our study identifies novel roles for KIN10 and TPS1 in mediating a signal that underlies sucrose-induced hypocotyl elongation in light/dark cycles.

## Introduction

Emerging seedlings monitor the environment to optimize their establishment and out-compete neighbouring plants (Salter et al., 2003; Weinig et al., 2007; Koini et al., 2009; Keuskamp et al., 2010; Crawford et al., 2012). Seedlings grow initially through cell expansion within the hypocotyl, which elongates rapidly to optimize light capture by the cotyledons. Hypocotyl elongation is controlled by several signalling pathways that converge upon phytohormones to regulate cell expansion (Lincoln et al., 1990; Collett et al., 2000). Examples of signals that adjust hypocotyl elongation include phytochrome-mediated signals concerning the ratio of red to far red light (R:FR) (Casal, 2013), blue light (Liscum and Hangarter, 1991), UV-B light (Kim et al., 1998; Hayes et al., 2014), temperature (Koini et al., 2009; Wigge, 2013; Mizuno et al., 2014), photoperiod and the circadian oscillator (Dowson-Day and Millar, 1999; Más et al., 2003; Nusinow et al., 2011). These signals are integrated by the PHYTOCHROME INTERACTING FACTOR (PIF)-family of basic helix-loop-helix transcription factors. The PIFs are signalling hubs that control plant development through genome-wide transcriptional alterations. One outcome of these PIF-mediated transcriptional changes are the alterations in phytohormone signalling that regulate hypocotyl elongation (Lorrain et al., 2008; Leivar and Quail, 2011).

Hypocotyl length is also increased by exogenous and endogenous sugars (Kurata and Yamamoto, 1998; Takahashi et al., 2003; Zhang et al., 2010; Liu et al., 2011; Stewart et al., 2011; Stewart Lilley et al., 2012; Zhang et al., 2015; Zhang et al., 2016). Under light/dark cycles, exogenous sugars are proposed to cause hypocotyl elongation by inducing auxin signals through the PIF-mediated gene regulation (Stewart et al., 2011; Stewart Lilley et al., 2012). Under extended darkness, brassinosteroid and GA phytohormones are involved in sugar-induced hypocotyl elongation, which may also involve the target of rapamycin (TOR) kinase regulator of energy- and nutrient-responses (Zhang et al., 2010; Dobrenel et al., 2011; Zhang et al., 2015; Zhang et al.,

2016). This elongation phenotype in darkness is thought to form a response to the starvation conditions that arise when plants are cultivated under periods of darkness exceeding the length of the daily light/dark cycle (Graf et al., 2010; Zhang et al., 2016). In comparison to these known roles for phytohormones and transcriptional regulators, the contribution of sugar sensing mechanisms to sucrose-induced hypocotyl elongation remain unknown.

Several sugar- or energy-signalling mechanisms underlie the metabolic and developmental responses of plants to sugars. One mechanism involves the Sucrose non-fermenting 1 (Snf1)-related protein kinase SnRK1 (Baena-González et al., 2007; Baena-González and Sheen, 2008), and another involves HEXOKINASE1 (Jang et al., 1997; Moore et al., 2003). SnRK1 controls metabolic enzymes directly by protein phosphorylation (Baena-González and Sheen, 2008). It also regulates > 1000 transcripts in response to carbohydrate availability, for example by adjusting bZIP transcription factor activity (Baena-González et al., 2007; Smeekens et al., 2010; Delatte et al., 2011; Matiolli et al., 2011; Mair et al., 2015). Both SnRK1- and hexokinase-mediated sugar signalling involve specific sugars functioning as signalling molecules that provide cellular information concerning sugar availability. For example, SnRK1 activity is thought to be regulated by trehalose-6-phosphate (Tre6P), whose concentration tracks the cellular concentration of sucrose (Lunn et al., 2006; Zhang et al., 2009; Nunes et al., 2013; Yadav et al., 2014). Tre6P is synthesized from UDP glucose and glucose-6-phosphate, which are derived from mobilized and transported sucrose, and also directly from photosynthesis. In Arabidopsis (*Arabidopsis thaliana*), Tre6P is synthesized by trehalose-6-phosphate synthase (TPS). Of 11 TPS homologs encoded by the Arabidopsis genome, TREHALOSE-6-PHOSPHATE SYNTHASE1 (TPS1) synthesizes Tre6P in plants (Gómez et al., 2010; Vandesteene et al., 2010), and TPS2 and TPS4 are catalytically active in yeast complementation assays (Delorge et al., 2015). Tre6P is believed to regulate SnRK1-mediated signalling by suppressing the activity of SNF1-RELATED PROTEIN KINASE1.1

(KIN10/AKIN10/SnRK1.1), which is a catalytic subunit of SnRK1 that is fundamental to the signalling role of SnRK1 (Baena-González et al., 2007; Zhang et al., 2009; Nunes et al., 2013). Manipulation of Tre6P metabolism in plants alters developmental phenotypes. For example, *tps1* knockout mutants undergo seedling developmental arrest (Gómez et al., 2006), expression of bacterial Tre6P synthase (*otsA*) or phosphatase (*otsB*) affects leaf senescence (Wingler et al., 2012), and Tre6P and KIN10 act within a photoperiod-response pathway that controls the induction of flowering (Baena-González et al., 2007; Gómez et al., 2010; Wahl et al., 2013). Signalling by Tre6P and KIN10 is also important for the regulation of growth rates. Growth is increased by sucrose in the presence of Tre6P (Schluepmann et al., 2003; Paul et al., 2010), but the lack of a quantitative (correlative) relationship between relative growth rates and [Tre6P] suggests that a threshold [Tre6P] is required for growth to occur (Nunes et al., 2013). Therefore, it has been suggested that control of KIN10/11 by [Tre6P] may 'prime' the regulation of growth-related genes to capitalize upon increased energy availability, rather than by inducing growth directly (Nunes et al., 2013). Remarkably, the impact of this pathway is sufficiently global that its manipulation can increase maize yields by almost 50% (Nuccio et al., 2015) and increase the yield and drought tolerance of wheat (Griffiths et al., 2016).

Given the importance of Tre6P metabolism and SnRK1 for growth regulation under cycles of light and dark, we wished to determine whether this energy-signalling mechanism is important for the regulation of sucrose-induced hypocotyl elongation. Moreover, because Tre6P signalling is reported to act upon GA and auxin signalling genes (Paul et al., 2010; Li et al., 2014) and these phytohormones are involved in sucrose-induced hypocotyl elongation (Zhang et al., 2010; Stewart Lilley et al., 2012), we reasoned that SnRK1 might act upon these phytohormones to regulate sucrose-induced hypocotyl elongation.

Here, we identified a novel role for Tre6P and KIN10 in the mechanisms that cause sucrose-induced hypocotyl elongation. We focused upon light/dark cycles rather than conditions of extended darkness (Zhang et al., 2010; Zhang et al., 2015; Zhang et al., 2016), because we wished to identify mechanisms that regulate growth and development under regimes more representative of real-world growing conditions that do not elicit prolonged starvation. We found that the sensitivity of hypocotyl elongation to sugars depends on the photoperiod and light intensity. We identified that KIN10 is important for expression of transcripts encoding auxin-induced expansins. Our data reveal a new mechanistic link between carbohydrate supply, energy sensing and phytohormone signalling during seedling emergence.

## Results

### *KIN10 and TPS1 are required for sucrose-induced hypocotyl elongation in light/dark cycles*

We investigated whether KIN10 and TPS1 contribute to sucrose-induced hypocotyl elongation under light/dark cycles (Kurata and Yamamoto, 1998; Takahashi et al., 2003; Stewart et al., 2011; Stewart Lilley et al., 2012). We studied hypocotyl elongation in transgenic Arabidopsis where KIN10 activity was manipulated by overexpressing the catalytic subunit of KIN10 (KIN10-ox) (Baena-González et al., 2007). Although KIN10 activity is regulated post-translationally by Tre6P (Zhang et al., 2009), KIN10 overexpression alone alters the abundance of energy-response transcripts in protoplasts (Baena-González et al., 2007). We used KIN10 overexpression rather than knockouts, because KIN10/11 double knockouts disrupt pollen production and are lethal (Zhang et al., 2001; Baena-González et al., 2007). We also used hypomorphic TILLING (targeted induced local lesions in genomes) mutants with reduced TPS1 activity (*tps1*-11, *tps1*-12) (Gómez et al., 2006; Gómez et al., 2010), which is preferable to *tps1* loss-of-function mutants that cause seedling developmental arrest (Gómez et al., 2006).

First, we investigated the effect of exogenous sucrose upon hypocotyl elongation in a variety of photoperiods (Fig. 1). Under 4 h and 8 h photoperiods, sucrose supplementation of wild type seedlings caused a significant increase in hypocotyl length relative to the sorbitol control (2.1-fold and 2.3-fold relative to sorbitol controls, under 4 h and 8 h photoperiods respectively) (Fig. 1A-E). In comparison, under 16 h photoperiods and constant light conditions exogenous sucrose did not promote hypocotyl elongation (Fig. 1A-E).

Next, we investigated roles of KIN10 in sucrose-induced hypocotyl elongation under light/dark cycles. Under 8 h photoperiods, the hypocotyls of two KIN10-ox lines (Baena-González et al., 2007) did not elongate significantly in response to exogenous sucrose relative to the MS control (Fig. 1B). Both KIN10-ox lines elongated 1.5-fold in response to sucrose relative to the sorbitol control (Fig. 1B). Exogenous sucrose caused no significant increase in the hypocotyl length of KIN10-ox seedlings under 4 h photoperiods (Fig. 1C). Hypocotyls of the L. *er.* background and KIN10-ox appeared shorter when supplemented with exogenous sucrose in constant light and 16 h photoperiods. However, this could be an osmotic effect rather than a sucrose response because hypocotyl elongation responded identically to sucrose and the sorbitol control (Fig. 1B).

Since KIN10 activity is thought to be regulated by Tre6P (Zhang et al., 2009), we investigated the role of the Tre6P biosynthetic enzyme TPS1 in sucrose-induced hypocotyl elongation under light/dark cycles. In two *tps1* TILLING mutants under 8 h photoperiods, sucrose supplementation caused a significant 2.3-fold increase in hypocotyl length in the wild type relative to the sorbitol control, compared with 1.6-fold and 1.3-fold increases in hypocotyl length in *tps1*-11 and *tps1*-12 respectively (Fig. 1D). Under 4 h photoperiods, sucrose caused a significant 2-fold increase in hypocotyl length of the wild type relative to the sorbitol control, compared with no significant increase in length in *tps1*-11 and a significant 1.5-fold increase in hypocotyl length in *tps1*-12 (Fig. 1E). Together, these experiments with KIN10 overexpressors and *tps1* mutants indicate that TPS1

and KIN10 are involved in one or more mechanisms that increase hypocotyl length in response to exogenous sucrose. This suggests that SnRK1-mediated energy signalling regulates hypocotyl elongation in response to sucrose supplementation.

*HEXOKINASE1 is not required for sucrose-induced hypocotyl elongation under light/dark cycles*

Hexokinase is thought to function as a sugar sensor that regulates development in response to the concentration of glucose (Jang et al., 1997; Moore et al., 2003), so we investigated whether hexokinase-based signalling also contributes to sucrose-induced hypocotyl elongation. For this, we measured the elongation of hypocotyls in response to exogenous sucrose in the *glucose insensitive2* (*gin2*-1) mutant of HEXOKINASE1. Overall, *gin2*-1 hypocotyls were slightly shorter than the wild type under all conditions tested (Fig. 1F). Exogenous sucrose caused a significant increase in hypocotyl length of wild type and *gin2*-1 seedlings, producing hypocotyls 63% and 67% longer than the osmotic control in the wild type and *gin2*-1, respectively (Fig. 1F). Therefore, sucrose caused a similar magnitude of hypocotyl elongation in *gin2*-1 and the wild type. This suggests that interconversion of sucrose to glucose, and therefore hexokinase-based glucose signalling, does not contribute to sucrose-induced hypocotyl elongation in short photoperiods.

*Relationship between day-length, light intensity and sucrose-induced hypocotyl elongation*

Our data suggest that the magnitude of the sucrose-induced increase in hypocotyl length depends upon the photoperiod or the quantity of light received. In the wild type, sucrose increased hypocotyl length under short (4 h or 8 h) but not long (16 h or constant light) photoperiods under photosynthetically active radiation (PAR) of 100 µmol $m^{-2}$ $s^{-1}$ (Fig. 1B-E, Fig. 2A). In addition, sucrose caused significantly greater hypocotyl elongation under 4 h photoperiods compared with 8 h photoperiods of 100 µmol $m^{-2}$ $s^{-1}$ (Fig. 2A). We reasoned that these varying responses to sucrose might arise from differences in total daily PAR received under each of these conditions, or

191 alternatively from the sensing of photoperiod length. To investigate this we compared the
192 magnitude of sucrose-induced hypocotyl elongation under the same total daily integrated PAR,
193 under longer photoperiods (16 h at 40 µmol $m^{-2}$ $s^{-1}$ and 8 h at 80 µmol $m^{-2}$ $s^{-1}$) and under shorter
194 photoperiods (8 h at 40 µmol $m^{-2}$ $s^{-1}$ and 4 h at 80 µmol $m^{-2}$ $s^{-1}$). Under a 16 h photoperiod at
195 40 µmol $m^{-2}$ $s^{-1}$, sucrose caused a significant increase in hypocotyl length (Fig. 2B, C). This
196 contrasts a 16 h photoperiod at 100 µmol $m^{-2}$ $s^{-1}$, where sucrose did not promote hypocotyl
197 elongation (Fig. 1, Fig. 2A). This suggests that the quantity of light received influences the
198 sensitivity of hypocotyl elongation to sucrose. Under 8 h photoperiods, sucrose caused greater
199 hypocotyl elongation under 40 µmol $m^{-2}$ $s^{-1}$ (mean 4.1 mm increase) than under 80 µmol $m^{-2}$ $s^{-1}$
200 (mean 3.3 mm increase), which also suggests that hypocotyl elongation is more responsive to
201 sucrose under lower light conditions (Fig. 2B, D). When daily integrated PAR was the same under
202 4 h and 8 h photoperiods, there was no difference in the increase in hypocotyl length caused by
203 sucrose (Fig. 2D, E). These responses suggest that daily integrated PAR influences the magnitude
204 of sucrose-induced hypocotyl elongation. However, the magnitude of sucrose-induced hypocotyl
205 elongation was significantly less under 16 h photoperiods at 40 µmol $m^{-2}$ $s^{-1}$ than 8 h photoperiods
206 at 80 µmol $m^{-2}$ $s^{-1}$ (Fig. 2B, C), suggesting that under long photoperiods, the magnitude of sucrose-
207 induced hypocotyl elongation could be also determined by a photoperiod-response mechanism
208 acting independently from daily integrated PAR. These data provide the insight that the
209 photoperiod-sensitivity of sucrose-induced hypocotyl elongation is determined by both the absolute
210 photoperiod and the amount of light received.

211 *Interaction between hypocotyl elongation by exogenous sucrose and the circadian oscillator*
212 The circadian oscillator regulates hypocotyl elongation because the accumulation of PIF proteins is
213 restricted to the end of the night (Nozue et al., 2007; Nusinow et al., 2011). Since the circadian

oscillator responds to exogenous and endogenous sugars (Dalchau et al., 2011; Haydon et al., 2013) and KIN10 overexpression can lengthen circadian period (Shin et al., 2017), we investigated whether sucrose-induced increases in hypocotyl length under short photoperiods involve the circadian oscillator. First, we tested whether the circadian oscillator components CIRCADIAN CLOCK ASSOCIATED1 (CCA1), LATE ELONGATED HYPOCOTYL (LHY) and TIMING OF CAB2 EXPRESSION1 (TOC1) are required for sucrose-induced hypocotyl elongation using the *cca1*-11 *lhy*-21 *toc1*-21 triple mutant (Ding et al., 2007). *cca1*-11 *lhy*-21 *toc1*-21 causes circadian arrhythmia under constant light and temperature, and disrupts rhythms of oscillator transcripts, including evening complex components that regulate hypocotyl elongation (Ding et al., 2007). Under 4 h photoperiods, the magnitude of the sucrose-induced increase in hypocotyl length was unaltered in *cca1*-11 *lhy*-21 *toc1*-21 (Fig. 3A; Fig. S1). Under 4 h photoperiods the hypocotyls of *cca1*-11 *lhy*-21 *toc1*-21 were of similar length to the wild type (Fig. 3A), whereas under 8 h photoperiods, *cca1*-11 *lhy*-21 *toc1*-21 has longer hypocotyls than the wild type (Ding et al., 2007). We also investigated whether two proteins that confer sugar sensitivity to the circadian oscillator, GIGANTEA (GI) and PSEUDO-RESPONSE REGULATOR7 (PRR7) (Dalchau et al., 2011; Haydon et al., 2013), contribute to sucrose-induced hypocotyl elongation under short photoperiods. We tested this because the *prr7*-11 mutation renders the oscillator insensitive to sugar signals that entrain the oscillator (Haydon et al., 2013), and the *gi*-11 mutation alters oscillator responses to long-term exposure to exogenous sucrose (Dalchau et al., 2011). In all cases, *gi*-11 had longer hypocotyls than the wild type (Fig. 3B), but the magnitude of the sucrose-induced increase in hypocotyl length was unaltered in *gi*-11 relative to the wild type (Fig. 3D). Likewise, the *prr7*-11 mutant also did not alter the magnitude of sucrose-induced increases in hypocotyl length (Fig. 3C, D).

These experiments indicate that two mechanisms providing sugar inputs to the circadian oscillator (Dalchau et al., 2011; Haydon et al., 2013) and three core oscillator components do not contribute to sucrose-induced increases in hypocotyl length under short photoperiods.

*Phytohormone signalling and sucrose-induced hypocotyl elongation under light/dark cycles: auxin*

Sucrose-induced hypocotyl elongation in the light involves auxin and GA signalling (Zhang et al., 2010; Stewart Lilley et al., 2012). We investigated the involvement of phytohormones in sucrose-induced hypocotyl elongation under light/dark cycles, and their relationship with SnRK1-mediated signalling. First, we examined the effect of the inhibitor of polar auxin transport 1-N-naphthylpthalamic acid (NPA) upon sucrose-induced hypocotyl elongation. NPA inhibited sucrose-induced hypocotyl elongation in a concentration-dependent manner, such that 10 μM NPA completely abolished sucrose-induced elongation (Fig. 4A). Consistent with previous work (Stewart Lilley et al., 2012), this indicates that under light/dark cycles sucrose-induced hypocotyl elongation is auxin-dependent. Next, we examined the responses of auxin- and PIF-dependent expansin transcripts to sucrose. Expansins are a large family of cell-wall modifying enzymes that allow turgor-driven cell expansion, and some expansin transcripts are upregulated by auxins in a PIF-dependent manner during hypocotyl elongation (Li et al., 2002; Miyazaki et al., 2016; Gangappa and Kumar, 2017). We examined *EXPANSIN A4* (*EXPA4*), *EXPA8* and *EXPA11* transcripts, which are auxin-induced in seedlings (Goda et al., 2004; Esmon et al., 2006; Winter et al., 2007; Lee et al., 2009). *EXPA8* and *EXPA11* transcripts were upregulated by conditions of constant darkness, which also increases hypocotyl elongation (Fig. S2A) (Boylan and Quail, 1991), and downregulated by 10 μM NPA, which suppresses hypocotyl elongation (Fig. S2B) (Stewart Lilley et al., 2012). *EXPA4* was unaltered by these conditions (Fig. S2). Therefore, *EXPA8* and *EXPA11* transcript abundance was increased by conditions that promote hypocotyl elongation, and

reduced by conditions that suppress hypocotyl elongation. Next, we monitored the change in abundance of these two expansin transcripts in response to sucrose under 4 h photoperiods. In the wild type, *EXPA11* transcripts were upregulated by 3% sucrose, whereas *EXPA8* transcripts were not upregulated by sucrose relative to the controls (Fig. 4B-E). In KIN10-ox, where sucrose does not promote hypocotyl elongation under light/dark cycles, *EXPA8* and *EXPA11* transcripts were not increased by sucrose (Fig. 4B-E). *EXPA8* was sucrose-induced relative to the controls in *tps1*-11, but not in *tps1*-12 (Fig. 4B, C). *EXPA11* transcripts were sucrose-induced in both *tps1*-11 and *tps1*-12 (Fig. 4D, E). The induction of these two expansin transcripts by sucrose in *tps1* mutants was unexpected, because both KIN10-ox and *tps* mutants suppress sucrose-induced hypocotyl elongation under short photoperiods (Fig. 1). We also examined several other transcripts associated with auxin biosynthesis or responses, but the osmotic controls caused substantial alterations in transcript abundance that prevented interpretation of their regulation by sucrose (Fig. S3).

*Phytohormone signalling and sucrose-induced hypocotyl elongation under light/dark cycles: gibberellins*

We tested whether GA signalling also contributes to sucrose-induced hypocotyl elongation under short photoperiods. After germination, wild type seedlings were transferred to media containing 3% sucrose or an osmotic control, supplemented with combinations of the GA biosynthesis inhibitor paclobutrazol (PAC), GA, or a carrier control. Consistent with previous studies, wild type seedlings grown on media supplemented with PAC or PAC and GA had significantly shorter hypocotyls than controls (Fig. 5A) (Cowling and Harberd, 1999; Liu et al., 2011). PAC abolished sucrose-induced hypocotyl elongation, with a small hypocotyl length rescue occurring when GA was supplied in combination with PAC (Fig. 5A). We confirmed that the GA was active by

demonstrating that, consistent with previous reports (Cowling and Harberd, 1999), hypocotyl length is increased by GA supplementation (Fig. S4).

GA increases growth by causing degradation of DELLA growth repressor proteins, and also through DELLA-independent mechanisms (Peng et al., 1997; Fu et al., 2002; Cheng et al., 2004; Cao et al., 2006). Therefore, we investigated the involvement of DELLA proteins in sucrose-induced hypocotyl elongation under light/dark cycles. The *gai*-1 mutant harbours a deletion within the DELLA domain of *GIBBERELLIC ACID INSENSITIVE* (*GAI*), which prevents GA-induced proteasomal degradation of GAI (Peng et al., 1997; Fu et al., 2002). Under 4 h photoperiods, sucrose supplementation increased hypocotyl length in *gai*-1, but the magnitude of sucrose-induced elongation in *gai*-1 was reduced compared with the wild type (hypocotyls became 36.5% longer in *gai*-1 in response to sucrose, compared with 59.2% longer in the wild type) (Fig. 5B). Under 16 h photoperiods, sucrose did not induce hypocotyl elongation in the wild type or *gai*-1 (Fig. 5B), which is consistent with Fig. 1B, C. We also examined the effect of a mutant lacking all five DELLA proteins upon sucrose-induced hypocotyl elongation under light/dark cycles (Koini et al., 2009). Under short photoperiods, sucrose-induced hypocotyl elongation was unaltered in this mutant (Fig. 5C). Interestingly, under long photoperiods sucrose promoted hypocotyl elongation in the DELLA global mutant, whereas sucrose was without effect upon wild type hypocotyls (Fig. 5C). The partial attenuation of sucrose-induced hypocotyl elongation in *gai*-1 (Fig. 5B) combined with the derepression of sucrose-induced hypocotyl elongation under long photoperiods in the DELLA global mutant (Fig. 5C) suggests that DELLA-mediated GA signalling contributes to, but does not exclusively control, sucrose-induced hypocotyl elongation.

*Phytohormone signalling and sucrose-induced hypocotyl elongation under light/dark cycles: abscisic acid*

ABA suppresses seedling development (Belin et al., 2009) and several studies have linked Tre6P and abscisic acid (ABA) signalling (Avonce et al., 2004; Ramon et al., 2007; Gómez et al., 2010; Debast et al., 2011). Therefore, we investigated whether ABA signalling contributes to sucrose-induced hypocotyl elongation under light/dark cycles. Sucrose-induced hypocotyl elongation was unaffected by the ABA receptor quadruple mutant *pyr1*-1 *pyl1*-1 *pyl2*-1 *pyl4*-1, which is highly ABA-insensitive (Park et al., 2009) (Fig. S5). This suggests that PYR/PYL-mediated ABA signalling does not participate in the mechanisms underlying sucrose-induced hypocotyl elongation under light/dark cycles.

## Discussion

*KIN10 and TPS1 contribute to sugar-induced hypocotyl elongation under light/dark cycles*

Here, we make the new finding that a mechanism involving KIN10 activity and Tre6P metabolism regulates sucrose-induced hypocotyl elongation under light/dark cycles. Whilst hypocotyl elongation arises from cell expansion rather than growth through increases in cell number (Gendreau et al., 1997), our data are consistent with studies demonstrating that Tre6P metabolism is a crucial regulator of growth responses to sucrose. For example, Arabidopsis seedlings overexpressing the bacterial Tre6P phosphatase *otsB*, which reduces [Tre6P], accumulate less biomass compared with the wild type when supplemented with sucrose (Schluepmann et al., 2003). The converse is also true; *otsA* (TPS) overexpressors, in which [Tre6P] is increased, accumulate more biomass than the wild type when supplemented with sucrose (Schluepmann et al., 2003). Therefore, our data using *tps1* mutants as a proxy for altered Tre6P metabolism provide new

evidence to support the notion that Tre6P promotes growth under conditions of increased sucrose availability (Schluepmann et al., 2003; Zhang et al., 2009).

Overexpression in Arabidopsis of the bacterial Tre6P synthase *otsA* has been reported to produce seedlings having shorter hypocotyls than the wild type (Paul et al., 2010). The sucrose-insensitivity of hypocotyl elongation in *tps1* mutants (Fig. 1) and the shorter hypocotyls in seedlings with increased [Tre6P] (otsA-ox) may appear to conflict with each other (Paul et al., 2010). However, the experiments are not directly comparable. We found that exogenous sucrose only caused hypocotyl elongation under short photoperiods or lower light conditions (Fig. 2). In comparison, the *otsA*-ox experiments involved 16 h photoperiods at higher PAR (150 µmol $m^{-2}$ $s^{-1}$) and shaking liquid culture (Zhang et al., 2009), both of which could mask the hypocotyl elongation response that we investigated.

Our experiments suggest that increased KIN10 activity might attenuate the elongation response of hypocotyls to exogenous sucrose under light/dark cycles. The KIN10-ox lines that we used overexpress the catalytic subunit of SnRK1 (Baena-González et al., 2007). KIN10 overexpression downregulates transcripts associated with anabolic processes and upregulates transcripts associated with energy starvation (Baena-González et al., 2007). Therefore, in our experiments KIN10 overexpression may have stopped seedlings from taking advantage of the greater energy availability caused by sucrose supplementation, so preventing sucrose-induced hypocotyl elongation in KIN10-ox (Fig. 1).

*Photoperiod-dependency of sugar-induced hypocotyl elongation*

We made the new finding that under relatively high light, exogenous sucrose increases hypocotyl length in photoperiods of 8 h and shorter, but not under long photoperiods or constant light (Fig. 1, Fig. 2). These data reconcile differences between previous studies of sucrose-induced hypocotyl

348 elongation. Previous studies reporting sucrose-insensitivity of hypocotyl elongation in the light
349 were conducted in continuous light (Zhang et al., 2010), in which we also found sucrose to be
350 without effect upon hypocotyls (Fig. 1B, Fig. 2A). In comparison, studies reporting that sucrose
351 does promotes hypocotyl elongation in the light were conducted under 8 h photoperiods (Stewart et
352 al., 2011; Stewart Lilley et al., 2012), where we likewise found that sucrose causes hypocotyl
353 elongation (Fig. 1B, Fig. 2). Therefore, the sensitivity of hypocotyls to sucrose-induced elongation
354 depends upon the photoperiod or the amount of light received each day.
355 One explanation for this response could be that the daily quantity of light determines the magnitude
356 of sucrose-induced hypocotyl elongation through the accumulation of photosynthetic metabolites.
357 Our experiments indicate that under shorter photoperiods, the sensitivity of hypocotyl elongation to
358 sucrose depends upon the total amount of daily light (Fig. 2A, D, E). Furthermore, sucrose-induced
359 hypocotyl elongation under long photoperiods only occurred when the seedlings were under lower
360 light conditions (Fig. 2A, B, C). One interpretation is that under long photoperiods and higher light,
361 cells are replete with sugars (Sulpice et al., 2014) therefore supplementation with exogenous
362 sucrose has a relatively small effect upon the hypocotyl length of already sugar-rich seedlings. In
363 contrast, under short photoperiods or lower light the background level of endogenous sugar is
364 lower (Sulpice et al., 2014), so supplementation with exogenous sucrose has a greater effect upon
365 hypocotyl length.
366 An alternative interpretation is that PIFs integrate light signals derived from photoreceptors with
367 SnRK1-mediated sugar signals to modulate the sensitivity of elongating hypocotyls to sucrose,
368 because PIFs are required for sucrose-induced hypocotyl elongation (Stewart et al., 2011; Stewart
369 Lilley et al., 2012). This might explain the PAR-independent reduction in sucrose-induced
370 hypocotyl elongation that occurred under long photoperiods (Fig. 2C). In the future, it will be
371 informative to resolve the relative contributions of these mechanisms to sucrose-induced hypocotyl

elongation, given that Tre6P can regulate expression of both PIFs and auxin signalling genes (Paul et al., 2010). This could provide insights into the nature of the coupling of SnRK1-mediated sugar signalling and growth regulation by PIFs (Paul et al., 2010; Stewart et al., 2011; Stewart Lilley et al., 2012).

*Involvement of phytohormone signals in sucrose-induced hypocotyl elongation under light/dark cycles*

Auxin, GA and brassinosteroids are reported to mediate sucrose-induced hypocotyl elongation, with a role for auxin identified under light/dark cycles and roles for GA and brassinosteroids identified under extended darkness (de Lucas et al., 2008; Zhang et al., 2010; Liu et al., 2011; Stewart et al., 2011; Stewart Lilley et al., 2012; Zhang et al., 2015; Zhang et al., 2016). Consistent with this, our data indicate that auxin signalling has a major role in sucrose-induced hypocotyl elongation under light/dark cycles (Fig. 4A), with GA signalling also contributing to this process (Fig. 5B, C). We suggest two possible reasons why paclobutrazol completely abolished sucrose-induced hypocotyl elongation (Fig. 5A), whereas the *gai*-1 mutant only led to partial inhibition of this phenotype (Fig. 5B). One possibility is that DELLA-independent GA signalling contributes to sucrose-induced hypocotyl elongation, since DELLA proteins control around 40-60% of GA-regulated transcripts (Cao et al., 2006). An alternative possibility is that these were off-target or ectopic effects of paclobutrazol, because the paclobutrazol-induced attenuation of hypocotyl elongation was not rescued fully by GA supplementation (Fig. 5A).

Auxin-induced expansins that are upregulated during hypocotyl elongation were also induced by sucrose supplementation (Fig. 4B-E; Fig. S2). Whilst *EXPA11* was induced strongly by sucrose, the small response of *EXPA8* to sucrose in the wild type makes it difficult to interpret the responses of *EXPA8* to sucrose in KIN10-ox and the *tps1* mutants (Fig. 4B, C). Interestingly, sucrose

induction of *EXPA11* was abolished in KIN10-ox, suggesting a role for KIN10 in expansin gene expression within elongating hypocotyls. In comparison, these expansins were sucrose-inducible in *tps1*-11 and *tps1*-12 (Fig. 4B-E). One possible explanation is that KIN10-ox causes a much greater level of SnRK1 activity compared with the *tps* mutants, which are hypomorphic alleles that harbour reduced Tre6P concentrations (Gómez et al., 2010) and are not completely deficient in sucrose-induced hypocotyl elongation (Fig. 1D, E).

An alternative and speculative explanation for the different behaviour of expansin transcripts in KIN10-ox and *tps* mutants could relate to Tre6P-KIN10 regulating growth through two broad processes- firstly, though direct signalling effects upon growth (e.g. by regulating auxin signals), and secondly through metabolic effects, such as growth constraints due to altered nocturnal catabolism. This could point to TPS1 and SnRK1 making independent contributions to sucrose-induced hypocotyl elongation under light/dark cycles, potentially through separate signalling and metabolic effects, rather than acting in series. Our data suggest that sucrose-induced hypocotyl elongation under light/dark cycles includes a signalling effect, previously proposed to occur through PIF-regulated auxin signals (Stewart et al., 2011; Stewart Lilley et al., 2012). On the other hand, the unexpected behaviour of expansin transcripts in *tps1* mutants (Fig. 1D, E) suggests that mechanisms additional to auxin/GA signalling might contribute to sucrose-induced hypocotyl elongation under light/dark cycles. These additional mechanisms could involve brassinosteroid and/or TOR signalling, which are required for sucrose-induced increases in hypocotyl length under extended darkness (Zhang et al., 2015; Zhang et al., 2016). It would be informative in future to investigate the crosstalk between SnRK1 and TOR energy signalling during hypocotyl elongation, to gain insights into the relative importance of these energy management pathways to the below-ground (darkness) and above-ground (light/dark cycles) stages of seedling establishment.

*Conclusions*

We identified a novel role for the SnRK1 energy signalling hub in the regulation of sucrose-induced hypocotyl elongation under light/dark cycles. We propose that KIN10 could be positioned upstream from the auxin and GA signals that lead to sucrose-induced hypocotyl elongation in the light (Liu et al., 2011; Stewart et al., 2011; Stewart Lilley et al., 2012). A question for future investigation concerns the functional organization of this pathway. In one scenario, KIN10-mediated energy signalling regulates hypocotyl elongation by acting upon phytohormone signalling, potentially through PIFs (Stewart Lilley *et al.*, 2012). In a different and non-exclusive scenario, SnRK1-mediated alterations in metabolic enzyme activity and growth-related transcripts prime hypocotyls to capitalize upon increased sucrose availability (Nunes *et al.*, 2013a). This is an interesting question in the case of hypocotyl elongation, which arises from cell expansion rather than growth through cell division and biomass accumulation *per se* (Gendreau *et al.*, 1997). These two possibilities are non-exclusive, because the phenotypic differences that we report between KIN10-ox lines and *tps1* mutants (e.g. expansin transcript accumulation; Fig. 4) could implicate more than one mechanism in sucrose-induced hypocotyl elongation.

A further question for future investigation is of the nature of the interplay between KIN10/Tre6P, TOR and brassinosteroids in the regulation of hypocotyl elongation in response to sugars. One speculative hypothesis is that under conditions of starvation, such as when a developing below-ground seedling is exhausting its seed-based energy store, brassinosteroid signalling produces a strong elongation cue to drive seedling emergence into the light (Zhang et al., 2015; Zhang et al., 2016). Then, once the seedling has emerged into the daily cycles of light and dark, KIN10/Tre6P adjusts the elongation of hypocotyls to allow optimal seedling establishment under local light conditions (Fig. 1, Fig. 2). It is possible that increased SnRK1 activity under conditions of transiently low light, for example due to unpredictable changes in the weather, operates alongside phototransduction pathways to prevent inappropriate etiolation following seedling emergence.

Therefore, one potential function of the mechanism that we identified might be to adapt the rate of seedling development to optimize the use of seed and photosynthetic resources under fluctuating light environments.

## Materials and Methods

*Plant material and growth conditions*

Arabidopsis (*Arabidopsis thaliana* (L.) Heynh.) seeds were surface-sterilized and sown on half-strength Murashige & Skoog basal salt mixture (Duchefa, Netherlands) (0.5 MS) with 0.8% (w/v) agar (Noordally et al., 2013). Seeds were then stratified (3 days at 4 °C) and germinated and grown for 7 days under 100 µmol $m^{-2}$ $s^{-1}$ of white light at 19 °C, except Fig. 2B-E where PAR was reduced. Media was supplemented with either 3 % (w/v) sucrose (87.6 mM) or 87.6 mM sorbitol as an osmotic control, according to the experiment. For experiments investigating gibberellin signalling, media was supplemented with 20 µM paclobutrazol (PAC) and 100 µM gibberellic acid ($GA_3$ form) (both Sigma-Aldrich) with a methanol carrier. Paclobutrazol is effective for studies of GA signalling during development at the concentration of 20 µM (Penfield et al., 2004; MacGregor et al., 2015). For experiments investigating auxin signalling, media was supplemented with 1-N-naphthylphthalamic acid (NPA, Sigma-Aldrich) at up to 10 µM with a dimethylsulfoxide (DMSO) carrier. Controls were supplemented with the appropriate carrier at the same concentration as treatment media (0.1% (v/v) DMSO for NPA; 0.12% (v/v) methanol for PAC and GA).

To transfer growing seedlings to media containing GA or PAC, surface sterilized and stratified seeds were pipetted onto 1 µm pore-diameter nylon mesh (Normesh, UK), on top of 0.5 MS 0.8% (w/v) agar, and allowed to germinate for 3 days. Seedlings were then transferred to 0.5 MS supplemented with either 3% (w/v) sucrose (87.6 mM) or 87.6 mM sorbitol, plus 20 µM PAC, 100

μM GA or both PAC and GA. Hypocotyls were measured after 5 days growth on treatment plates. For experiments with circadian oscillator mutants, we did not use arrhythmic CCA1-ox plants because overexpression of CCA1 causes very long hypocotyls (Wang and Tobin, 1998), which would confound investigation of the role of sugars in hypocotyl elongation.

Genotypes used were *tps1* TILLING mutants (Gómez et al., 2010), KIN10-ox (Baena-González et al., 2007), *gin2*-1 (Moore et al., 2003), *gai*-1 (Koorneef et al., 1985), DELLA global mutant (Koini et al., 2009), *pyr1 pyl1 pyl2 pyl4* (Park et al., 2009), *cca1*-11 *lhy*-21 *toc1*-21 (Ding et al., 2007), *gi*-11 (Richardson et al., 1998) and *prr7*-11 (Yamamoto et al., 2003; Nakamichi et al., 2005). In the KIN10-ox lines, *KIN10* transcript abundance was 17-fold greater than the wild type in elongating hypocotyls (Fig. S6A). In the *tps1*-11 and *tps1*-12 alleles, *TPS1* transcript abundance was unchanged (*tps1*-11) or slightly increased (*tps1*-12) compared with the wild type (Fig. S6B). This result for the *tps1* alleles was unsurprising because these are mis-sense mutants rather than insertion mutants (Gómez et al., 2010).

*Hypocotyl measurement*

Seedlings were grown on square petri dishes within temperature-controlled growth chambers (Panasonic MLR-352). Plates were angled at about 45 degrees to allow hypocotyls to elongate without touching lids. Hypocotyls were measured by positioning 7 day-old seedlings on the surface of 1% (w/v) agar for photography (Nikon D50) and subsequent measurement using the ImageJ software (https://imagej.nih.gov/ij/).

*RNA extraction and qRT-PCR*

RNA was extracted according to (Noordally et al., 2013), using the Machery-Nagel Nucleospin II plant RNA extraction kit incorporating DNase I treatment (Thermo-Fisher), except approximately 60 seedlings were used per RNA sample. cDNA was synthesized using the High Capacity cDNA

Reverse Transcription Kit with RNase Inhibitor (Applied Biosystems), according to manufacturer's instructions. cDNA was analyzed using an MXPro 3005 real time PCR system (Agilent) with Brilliant III Ultra-Fast SYBR qPCR mastermix (Agilent) (primers in Table S1). At least two technical repeats were performed for each qRT-PCR reaction. Data were analyzed using the ΔΔCt method, with *PROTEIN PHOSPHATASE 2A SUBUNIT A3* (*PP2AA3*) as a reference transcript.

**Supplemental Material**

**Figure S1.** The *cca1*-11 *lhy*-21 *toc1*-21 triple mutant does not alter sucrose-induced hypocotyl elongation (direct repeat of Figure 3A).

**Figure S2.** Selection of expansin transcripts for experimentation.

**Figure S3.** Sucrose supplementation of growth media did not alter abundance of auxin biosynthesis transcripts or auxin-responsive transcripts relative to osmotic controls.

**Figure S4.** Efficacy of $GA_3$ used for study.

**Figure S5.** ABA signalling is not required for sucrose-induced hypocotyl elongation under short photoperiods.

**Figure S6**. *KIN10* and *TPS1* transcript abundance in KIN10-ox and *tps1* TILLING mutants.

**Table S1.** qRT-PCR primer sequences.

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**Figure legends**

**Figure 1.** KIN10 and TPS1 participate in sucrose-induced hypocotyl elongation. (A) Representative images of L. *er*. wild type, KIN10-ox and *tps1* seedlings cultivated under a variety of photoperiods, with and without supplementation with 3% sucrose. All panels scaled identically. Images are a subset of seedlings used to generate data in (B-E). (B-E) Lengths of hypocotyls of seedlings grown under (B, D) constant light, 16 h and 8 h photoperiods, and (C, E) 4 h photoperiods. Photoperiods are indicated underneath graphs. (F) Effect of sucrose supplementation upon *gin2*-1 hypocotyl length. S.E.M. is small under continuous light (0.03 – 0.05 mm), so not visible on graphs. Data were analysed with ANOVA and Tukey's post-hoc tests ($n$ = 10 (B-E) or $n$ = 20 (F) seedlings in three independent experiments, ± S.E.M). Different letters indicate statistically significant differences between means, specifically within each light condition ($p$ < 0.05). (B-E); MS is half-strength MS media, and Suc and Sor are 0.5 MS supplemented with 3% (w/v) sucrose or equimolar sorbitol (87.6 mM osmotic control), respectively.

**Figure 2.** Day-length dependency of sucrose-induced hypocotyl elongation in wild type seedlings. (A) Increase in hypocotyl length caused by sucrose under range of photoperiods (data derived from Fig. 1, plotted relative to sorbitol control). (B-E) Comparison of (B, D) absolute hypocotyl length

and (C, E) proportional increase in hypocotyl length caused by sucrose supplementation under specified photosynthetically active radiation (PAR) and photoperiod. Mean ± S.E.M; (A, C-E) $n$ = 10 seedlings in two independent experiments (B) $n$ = 20 seedlings. Data analysed using ANOVA followed by post-hoc Tukey test. Different letters indicate statistically significant differences between means ($p < 0.05$).

**Figure 3.** The circadian oscillator does not participate in sucrose-induced hypocotyl elongation under short photoperiods. Sucrose-induced change in hypocotyl length of (A) a circadian oscillator triple mutant (*cca1*-11 *lhy*-21 *toc1*-21, background Ws-2) and (B, C) two oscillator components participating in sucrose regulation of the circadian oscillator. (D) Change in hypocotyl length caused by sucrose supplementation in *gi*-11 and *prr7*-11, expressed relative to 0.5 MS control. MS is 0.5 MS media, and Suc and Sor are 0.5 MS supplemented with 3% (w/v) sucrose and sorbitol (87.6 mM, osmotic control), respectively. Data are mean ± S.E.M ($n$ = 10 – 16), analysed with (A-C) ANOVA and post-hoc Tukey tests and (D) two-sample t-test comparing mutant with wild type for each treatment. Data show one of three independent repeats of the experiment, conducted under 4 h photoperiods. Different letters indicate statistically significant differences between means ($p < 0.05$).

**Figure 4.** Auxin signalling underlies sucrose-induced hypocotyl elongation and KIN10 regulates expansin gene expression. (A) Hypocotyl length of seedlings cultivated with a range of concentrations of the inhibitor of polar auxin transport 1-N-naphthylphthalamic acid (NPA), under 4 h photoperiods (mean ± S.E.M; $n$ = 20). (B-E) Sucrose-induced changes in expansin transcript abundance in elongating wild type, *tps1* and KIN10-ox seedlings under 4 h photoperiods. (B, D) Indicate *EXPA8* and *EXPA11* transcript abundance relative to *PP2AA3* (mean ± S.E.M; $n$ = 3). (C,

E) Indicate the magnitude of sucrose-induced change in transcript abundance in each genotype relative to the osmotic control. Data analysed with ANOVA and post-hoc Tukey tests, and with statistical significance indicated using starring (N.S. = not significant $p > 0.05$; * = $p <= 0.05$; ** = $p < 0.01$; *** = $p < 0.001$).

**Figure 5.** Gibberellin signals contribute to sucrose-induced hypocotyl elongation under short photoperiods. (A) The GA biosynthesis inhibitor paclobutrazol (PAC) at 20 μM inhibits sucrose-induced hypocotyl elongation. Seedlings were germinated on MS agar and transferred to treatment media after germination; carrier control was 0.12% (v/v) methanol. (B) Sucrose-induced hypocotyl elongation was attenuated in *gai*-1 mutant seedlings. (C) Sucrose-induced hypocotyl elongation was unaltered in a DELLA global knockout mutant. Experiments performed under 4 h photoperiods. Data are mean ± S.E.M ($n = 20$) from one of two independent repeats, analysed with ANOVA and post-hoc Tukey tests. Different letters indicate statistically significant differences between means ($p < 0.05$). Osmotic control was 87.6 mM sorbitol.

**Supplemental Figure Legends**

**Figure S1.** The *cca1*-11 *lhy*-21 *toc1*-21 triple mutant does not alter sucrose-induced hypocotyl elongation under light/dark cycles. This is a direct repeat of the experiment in Figure 3A where data approach statistical significance. (A) Comparison of hypocotyl length of Ws-2 background and *cca1*-11 *lhy*-21 *toc1*-21 grown on 0.5 MS media (MS) and 0.5 MS media supplemented with 3% (w/v) sucrose (Suc); (B) Increase in hypocotyl length of wild type and *cca1*-11 *lhy*-21 *toc1*-21 caused by exogenous sucrose, relative to 0.5 MS control. Data are mean ± S.E.M; $n = 10$; statistical

583 significance from two-sample t-tests comparing mutant and wild type for each treatment; N.S. = no
584 significant difference ($p$ >= 0.05).
585
586 **Figure S2.** *EXPA8* and *EXPA11* transcripts were (A) up-regulated by conditions that promote
587 hypocotyl elongation (constant darkness) and (B) down-regulated by the auxin transport inhibitor
588 NPA (mean ± S.E.M.; $n$ = 3). Transcript abundance was relative to *PP2AA3* reference transcript
589 and used 7-day old L. *er*. seedlings. Data analysed with ANOVA followed by post-hoc Tukey test.
590 Different letters indicate statistically significant differences between means ($p$ < 0.05).
591
592 **Figure S3.** Sucrose supplementation did not alter the abundance of auxin biosynthesis transcripts
593 or auxin-responsive transcripts relative to osmotic controls, due to responses of osmotic controls.
594 Data indicate relative abundance of three auxin biosynthesis transcripts (*YUCCA8, YUCCA9,*
595 *CYP79B3*) and two auxin-responsive transcripts (*IAA29, SAUR15*) in two backgrounds, using
596 *PP2AA3* as the reference transcript. Seedlings (60 per replicate) were grown on 0.5 MS, 3% (w/v)
597 sucrose, or 87.6 mM sorbitol as osmotic control, and harvested for RNA 4 days and 7 days after
598 germination (indicated on x axis). Two background lines were used to evaluate whether there were
599 ecotype-specific phenotypes. Data are mean ± S.E.M; $n$ = 2 independent biological repeats.
600 Analyzed by ANOVA ($p$ >= 0.05 in all cases, i.e. not significant).
601
602 **Figure S4.** Confirmation of activity of $GA_3$. 100 µM $GA_3$ increased hypocotyl length relative to
603 the carrier control in both L. *er*. and Col-0 backgrounds, under 4 h and 16 h photoperiods.
604 Seedlings were germinated and grown in presence of GA. Data were collected during methods
605 development and are not directly comparable with other experiments. Data expressed as mean ±

S.E.M. ($n$ = 20) and analysed with ANOVA followed by post-hoc Tukey test. Different letters indicate statistically significant differences between means ($p < 0.05$).

**Figure S5.** ABA signalling is not required for sucrose-induced hypocotyl elongation under short photoperiods. The *pyr1*-1 *pyl1*-1 *pyl2*-1 *pyl4*-1 quadruple mutant incorporates Col-0 and L. *er.* backgrounds (Park et al., 2009), both of which are included as controls. Data indicate mean hypocotyl lengths of seedlings grown on 0.5 MS supplemented with 3% sucrose or an osmotic control (87.6 mM sorbitol), under 4 h photoperiods. Data are mean ± S.E.M.; $n$ = 20 (background lines); $n$ = 3 – 9 depending on treatment for *pyr1*-1 *pyl1*-1 *pyl2*-1 *pyl4*-1 (low replicate numbers due to poor mutant germination). Data are from one of two independent repeats. Statistical significance from independent-samples Kruskal-Wallis analysis of variance on ranks and post-hoc Dunn tests comparing mutant and wild type for each treatment; *** = $p < 0.001$; N.S. = no significant difference ($p >= 0.05$).

**Figure S6.** *KIN10* and *TPS1* transcript abundance KIN10-ox and *tps1* TILLING mutants. (A) KIN10 transcript abundance in two independent KIN10-ox lines (Baena-González et al., 2007), its L. *er* background, and also Col-0. Transcript abundance is relative to *PP2AA3* reference. (B) *TPS1* transcript abundance in *tps1*-11 and *tps1*-12 (Gómez et al., 2010), alongside the L. er and Col-0 backgrounds. Transcript abundance was measured in 7 day old seedlings and is relative to the *PP2AA3* reference transcript. Data expressed as mean ± S.E.M ($n$ = 3) and analyzed with ANOVA followed by post-hoc Tukey test. Different letters indicate statistically significant differences between means ($p < 0.05$).

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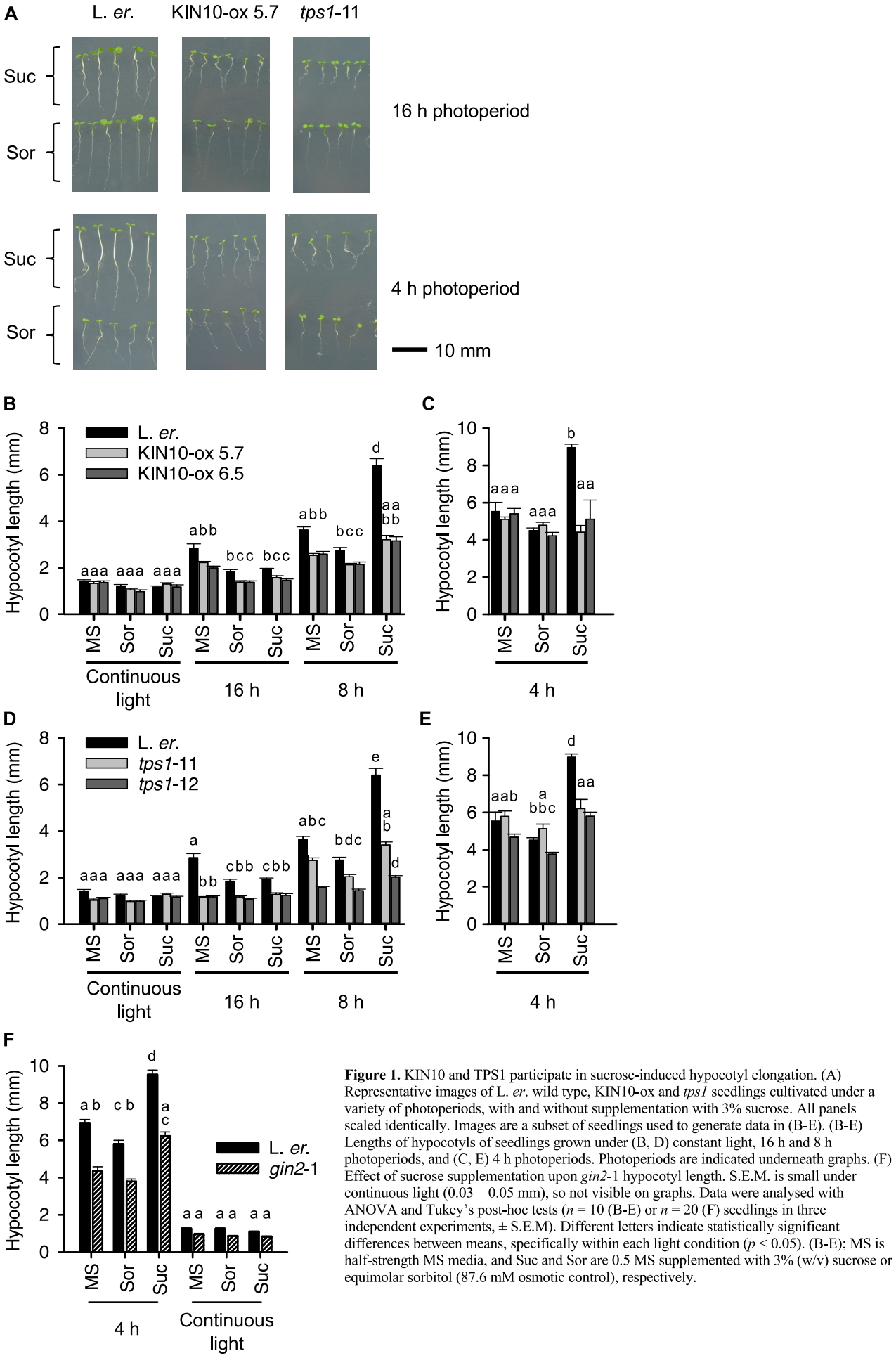


**Figure 1.** KIN10 and TPS1 participate in sucrose-induced hypocotyl elongation. (A) Representative images of L. *er*. wild type, KIN10-ox and *tps1* seedlings cultivated under a variety of photoperiods, with and without supplementation with 3% sucrose. All panels scaled identically. Images are a subset of seedlings used to generate data in (B-E). (B-E) Lengths of hypocotyls of seedlings grown under (B, D) constant light, 16 h and 8 h photoperiods, and (C, E) 4 h photoperiods. Photoperiods are indicated underneath graphs. (F) Effect of sucrose supplementation upon *gin2*-1 hypocotyl length. S.E.M. is small under continuous light (0.03 – 0.05 mm), so not visible on graphs. Data were analysed with ANOVA and Tukey's post-hoc tests ($n$ = 10 (B-E) or $n$ = 20 (F) seedlings in three independent experiments, ± S.E.M). Different letters indicate statistically significant differences between means, specifically within each light condition ($p < 0.05$). (B-E); MS is half-strength MS media, and Suc and Sor are 0.5 MS supplemented with 3% (w/v) sucrose or equimolar sorbitol (87.6 mM osmotic control), respectively.

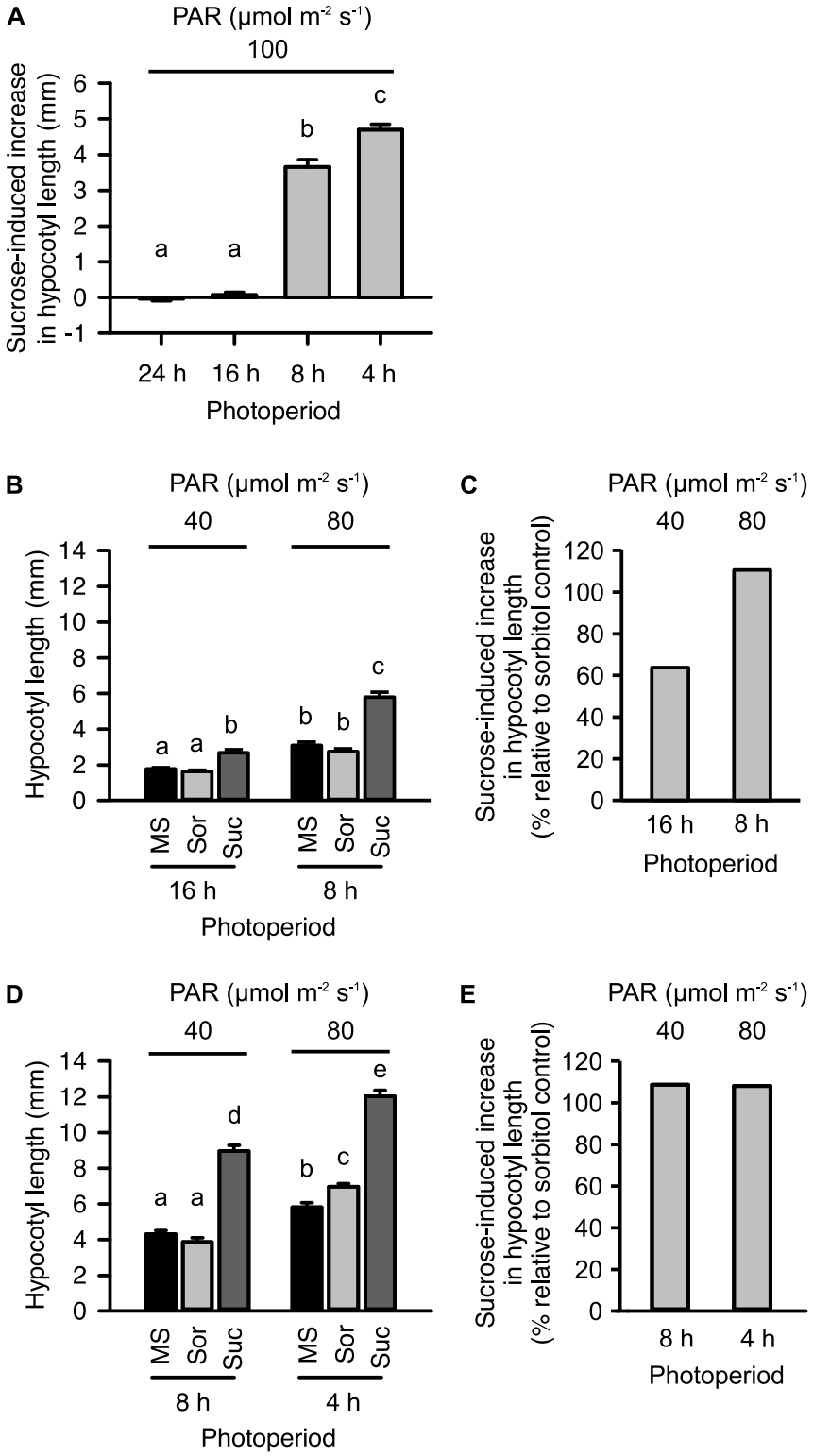


**Figure 2.** Day-length dependency of sucrose-induced hypocotyl elongation in wild type seedlings. (A) Increase in hypocotyl length caused by sucrose under range of photoperiods (data derived from Fig. 1, plotted relative to sorbitol control). (B-E) Comparison of (B, D) absolute hypocotyl length and (C, E) proportional increase in hypocotyl length caused by sucrose supplementation under specified photosynthetically active radiation (PAR) and photoperiod. Mean ± S.E.M; (A, C-E) $n = 10$ seedlings in two independent experiments (B) $n = 20$ seedlings. Data analysed using ANOVA followed by post-hoc Tukey test. Different letters indicate statistically significant differences between means ($p < 0.05$).

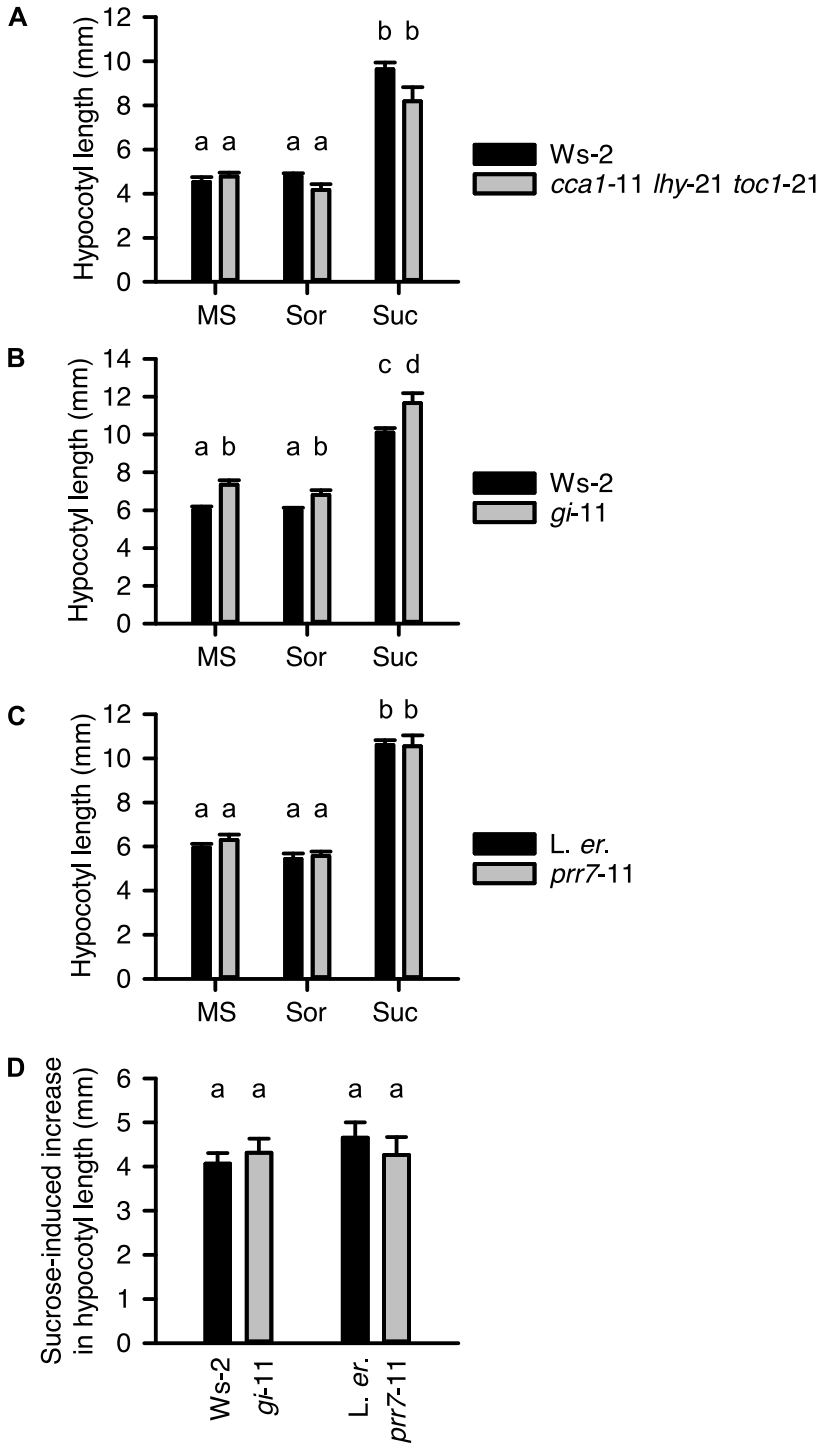


**Figure 3.** The circadian oscillator does not participate in sucrose-induced hypocotyl elongation under short photoperiods. Sucrose-induced change in hypocotyl length of (A) a circadian oscillator triple mutant (*cca1*-11 *lhy*-21 *toc1*-21, background Ws-2) and (B, C) two oscillator components participating in sucrose regulation of the circadian oscillator. (D) Change in hypocotyl length caused by sucrose supplementation in *gi*-11 and *prr7*-11, expressed relative to 0.5 MS control. MS is 0.5 MS media, and Suc and Sor are 0.5 MS supplemented with 3% (w/v) sucrose and sorbitol (87.6 mM, osmotic control), respectively. Data are mean ± S.E.M ($n$ = 10 – 16), analysed with (A-C) ANOVA and post-hoc Tukey tests and (D) two-sample t-test comparing mutant with wild type for each treatment. Data show one of three independent repeats of the experiment, conducted under 4 h photoperiods. Different letters indicate statistically significant differences between means ($p < 0.05$).

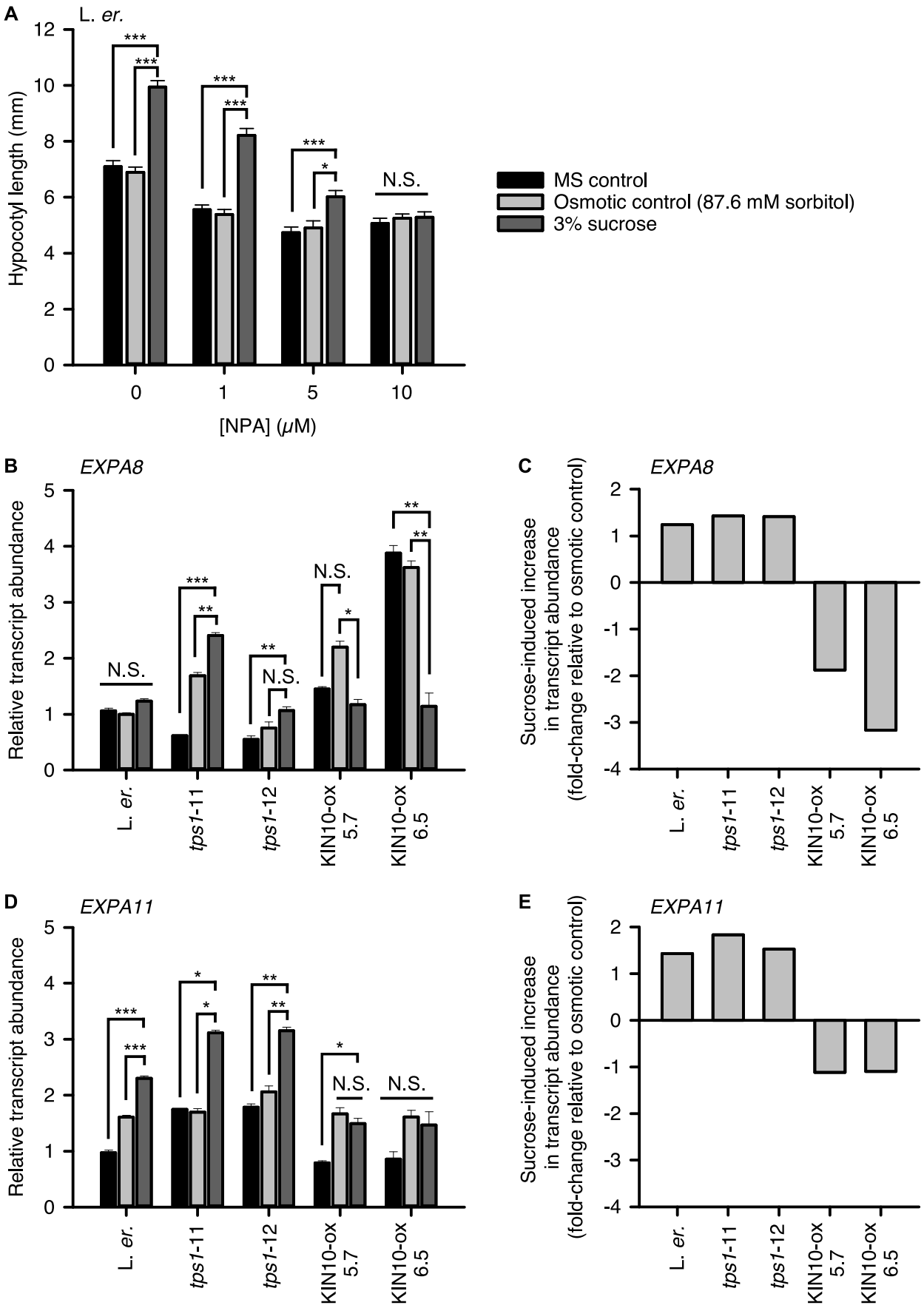


**Figure 4.** Auxin signalling underlies sucrose-induced hypocotyl elongation and KIN10 regulates expansin gene expression. (A) Hypocotyl length of seedlings cultivated with a range of concentrations of the inhibitor of polar auxin transport 1-N-naphthylphthalamic acid (NPA), under 4 h photoperiods (mean ± S.E.M; $n = 20$). (B-E) Sucrose-induced changes in expansin transcript abundance in elongating wild type, *tps1* and KIN10-ox seedlings under 4 h photoperiods. (B, D) Indicate *EXPA8* and *EXPA11* transcript abundance relative to *PP2AA3* (mean ± S.E.M; $n = 3$). (C, E) Indicate the magnitude of sucrose-induced change in transcript abundance in each genotype relative to the osmotic control. Data analysed with ANOVA and post-hoc Tukey tests, and with statistical significance indicated using starring (N.S. = not significant $p > 0.05$; * = $p <= 0.05$; ** = $p < 0.01$; *** = $p < 0.001$).

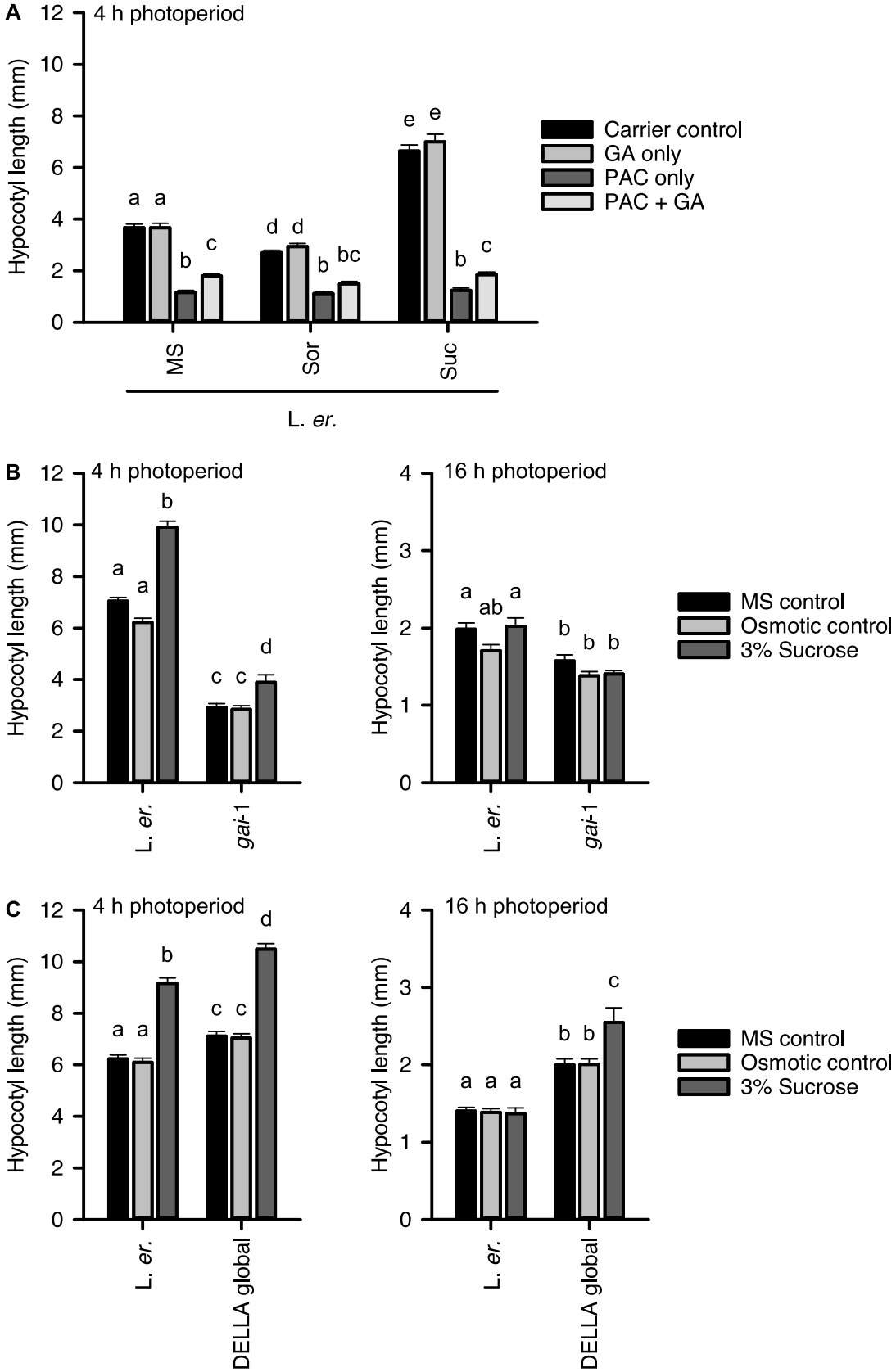


**Figure 5.** Gibberellin signals contribute to sucrose-induced hypocotyl elongation under short photoperiods. (A) The GA biosynthesis inhibitor paclobutrazol (PAC) at 20 μM inhibits sucrose-induced hypocotyl elongation. Seedlings were germinated on MS agar and transferred to treatment media after germination; carrier control was 0.12% (v/v) methanol. (B) Sucrose-induced hypocotyl elongation was attenuated in *gai*-1 mutant seedlings. (C) Sucrose-induced hypocotyl elongation was unaltered in a DELLA global knockout mutant. Experiments performed under 4 h photoperiods. Data are mean ± S.E.M ($n = 20$) from one of two independent repeats, analysed with ANOVA and post-hoc Tukey tests. Different letters indicate statistically significant differences between means ($p < 0.05$). Osmotic control was 87.6 mM sorbitol.

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